Orthographic influence on speech processing:

A combined TMS and behavioural study

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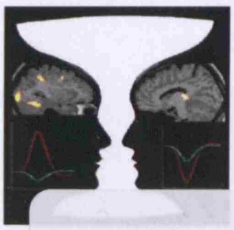

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"Setting an example is not the main means of influencing another, it is the only means. "

Albert Einstein

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fMRI:	functional magnetic resonance imaging
FOV:	field of view
FUS:	fusiform gyrus
FWHM:	full-width half-maximum
HRF:	hemodynamic response function
Hz:	Hertz
IPS:	intraparietal sulcus
LOC:	lateral occipital complex
M:	male
min:	minute
MR:	magnetic resonance
MRI:	magnetic resonance imaging
ms:	milliseconds
RT:	reaction times
rTMS:	repetitive transcranial magnetic stimulation
s:	seconds
SD:	standard deviation
SEM:	Standard error of the mean
SMG:	supramarginal gyrus
T1:	spin-lattice relaxation time
TE:	echo time
TMS:	transcranial magnetic stimulation
TR:	repetition time

Statement of Contributions

Study design:	Dr. Chotiga Pattamadilok, Iris N. Knierim, Dr. Joseph T. Devlin
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Abstract

Previous behavioural studies of auditory lexical decision have shown longer reaction times due to inconsistent spelling of a word's rime – the sound after the first consonant cluster (e.g.,-ight/-ite) - when compared to consistently spelt rimes (e.g.-ust). A possible explanation is that co-activation of orthographic representations during word processing is triggering the effect. An alternative account assumes that the process of learning to read and write contributed to the restructuring of phonological representations, such that inconsistent rimes induce competition of competing phonological representations reflected by longer reaction times. To test these hypotheses, we applied repetitive transcranial stimulation (rTMS) to the left supramarginal gyrus (SMG), to the left posterior fusiform gyrus (FUS) and two control sites.

Two experiments (n=47) were conducted applying rTMS (400ms of 10Hz at 100% motor threshold) to either SMG, FUS or a respective control site. A control task using auditory semantic categorisation was tested at the same site.

ANOVA [2(Stimulation) x 2(Site) x 2(Consistency)] run on the lexical decision reaction time data of the first experiment showed a three-way interaction; $F(1,16) = 7.2$, $p < .05$: the orthographic effect disappeared only when the stimulation was applied on SMG. No TMS effect was found in the control task regardless of the site of stimulation ($Fs < 1$).

Considering the SMG involvement in phonological processing, the data suggests that the consistency effect is mediated at a phonological level presumably because learning to read fundamentally reshapes phonological representations. TMS to SMG disrupts the processing advantage for consistent words by adding noise to performed computation, while TMS to FUS does not affect the consistency effect.

1. Introduction

A milestone in each child's development is the acquisition of language. From a very early age, humans start to express themselves and communicate with others by speaking and listening. It is considerably later in life, when most children become literate allowing them to read and write.

This priority of spoken over written language does not only hold for an individual's personal development, but is also mirrored in humankind's genesis of these abilities (Liberman, 1992). Even more, orthography seems not to be a necessary component of language, as various languages exist without writing systems (all sign languages, for instance). However, once literacy is acquired, written language plays an important role in daily living.

Not surprisingly, within the human language processing system, orthographic and phonological information are dealt with differently. They do have different input modalities (i.e. vision or audition) and also recruit different cortical areas. In this context, 'orthographic processing' refers to the processing of information encoded in the spelling structure of written language (Foorman, Francis, Fletcher, & Lynn, 1996; Juel, 1983; Perfetti, 1984), while 'phonological processing' deals with the processing of information that is encoded in the sound structure of spoken language (Campbell, 1992; Foorman, 1994; Wagner & Torgesen, 1987).

Clearly, orthographic and phonological processing interact with each other, as this is essential for reading aloud and dictation. However, phonological and orthographic information also influence each other in more subtle ways, such as processes which do not seem to require both modalities at first sight as deciding whether two auditory stimuli rhyme or not.

Seidenberg and Tanenhaus (1979) demonstrated that orthographic properties of words influence participants' reaction times during auditory rhyme judgements. Although no visual component was involved, participants decided that a word pair rhymed faster then when the pair had the same spelling (e.g. 'toast-roast') compared to rhyming word pairs with different spellings (e.g. 'toast-ghost'). In contrast, in non-rhyming trials, faster reaction times were observed when the spelling diverged (e.g. 'leaf-clef') compared to negative trials with the same spelling (e.g. 'leaf-deaf'). Their results were surprising, as rhyming pairs did not differ in their sound quality depending on spelling. Even so, the word's orthography influenced reaction times despite the fact that orthography was incidental to the task.

Since this first paper, many studies have confirmed orthographical influence on speech processing in various tasks (Frauenfelder, Segui, & Drijkstra, 1990; Cutler, Treiman, & Van Ooijen, 1998, Treiman, & Cassar, 1997, Treiman,1983, 1986, Ventura, Kolinsky, Brito-Mendes, & Morais, 2001, Chéreau, Gaskell & Dumay, 2006; Slowiaczek, Soltano, Wieting, & Bishop, 2003).

Consistency effect

One paradigm where orthographic consistency effects are robust is auditory lexical decision. In these experiments, subjects decide whether an auditorily presented stimulus is an existing word of a given language or whether it is a pseudoword – a pronounceable utterance close to a word but without any lexical meaning. Within this set-up, Ziegler and Ferrand (1998) were the first to demonstrate that reaction times differ with respect to the spelling of the rime – that is the phonological unit that refers to the sound pattern of a syllable from after its first consonant cluster to its end. In a monosyllabic word the rime is the word's sound from after the first consonant cluster till the end. For example, both 'clown' or brown' have the same rime 'own'. The spelling of a rime in a given language can either be always the same or it can be different. Homogenously spelt rimes are called consistent, while inconsistent is used to refer to rimes that can be spelt differently in different words (Table 1). Because the mapping between sound and spelling differs between languages, they also differ in the degree to which rimes are spelt consistently.

Table . Examples of consistent and inconsistent rimes in English.

Category	Rime	Example
consistent	-ust	must
	-ug	plug
inconsistent	-ea, -ee	plea, flee
	-ight, -ite	fight, kite

Ziegler and Ferrand (1998) found that, although no orthographic information was needed to perform the task, the latencies for words with inconsistent rimes were longer compared to those of words with consistent rimes. Additionally, the accuracy scores were lower in the inconsistent condition. The difference in mean reaction times between words with consistent rimes compared to words with inconsistent ones was subsequently called the orthographic consistency effect.

The orthographic consistency effect was replicated in subsequent studies which also demonstrated that the effect is not due to differences in word frequency, differences in phonological differences between consistent and inconsistent rimes, or a strategy used to simplify the task (Ventura, Morais, Pattamadilok, & Kolinsky, 2004; Ziegler, Ferrand, & Montant, 2004; Pattamadilok, Perre, Dufau, & Ziegler, 2008).

Interestingly, developmental studies (Ziegler & Muneaux, 2007) have revealed that the influence of orthography on spoken word recognition is tightly linked to becoming literate. By studying children prior to literacy and during the first years at school, it could be shown that the size of the feedback consistency effect can be predicted by a child's reading level. Several other studies provide additional evidence that a person's reading ability is directly linked to the occurrence and size of the consistency effect (Ventura, Morais, & Kolinsky, 2007; Miller & Swick, 2003; Morais, Cary, Alegria, & Bertelson, 1979).

Hypotheses

There are two hypotheses to explain the orthographic consistency effect which assume different implications of acquiring literacy. The first hypothesis (Slowiaczek *et al.*, 2003; Ziegler & Ferrand, 1998), referred to as 'co-activation hypothesis' or 'bimodal interactive activation account', assumes that each word possesses separate phonological and orthographic representations. However, the process of learning to read and write leads to strong and permanent associations between the phonological and the orthographic representation of a word, creating a single functional network (Perre & Ziegler, 2008). The processing of either a spoken or a written word then activates the word's whole network, including all connected representations. Thus, the orthographic features of a word would be activated whenever one processes a spoken word and vice versa. When a word with an inconsistent rime is processed, its inconsistent rime would activate different possible spelling patterns. This induces competition between them leading to more processing load and longer reaction times compared to the processing of a word with a consistent rime that only activated one spelling pattern. The orthographic consistency effect then results from competing orthographic representations for inconsistent rimes.

The second explanation, described as 're-shaping' or 'phonological restructuring account' focuses on the nature of the phonological representations after literacy is acquired rather than the interactions between the phonological and the orthographic representations (Harm & Seidenberg, 1999; Taft & Hambly, 1985; Taft, 2006). It is assumed that learning to read results in orthography re-shaping pre-existing phonological representations. By learning the orthographic structure of words, the phonological representations change to such an extent that they take the new knowledge about sound and the expression of sound through letters into account (Ehri & Wilce, 1980). Hence they are less close to the pure phonetic form of the word than before. Following this approach, phonological representations become more fine-grained if a consistent orthographical pattern for a phonological unit exists. This is due to stronger and more regular reinforcement from their orthographic counterpart. In contrast, heterogeneous orthographic representation of a rime weakens the development of a single abstract phonological representation because no consistent mapping can take place. Consequently, an abstract phonological representation for each of the spelling alternatives develops. During the processing of an inconsistent rime, these different abstract phonological representations compete with each other. The competition process leads to longer reaction times for the inconsistent rimes compared to consistent rimes, thus explaining the occurrence of the orthographic consistency effect.

Contrasting these two hypotheses, the co-activation hypothesis assumes that the processing of a spoken word automatically activates two different types of representations simultaneously, while the re-shaping hypothesis states that the orthographic representations are not activated during the task but had exerted their influence in the course of literacy acquisition so that multiple representations for inconsistent rimes have developed..

Although neither hypothesis is based on neuroimaging data, they both make predictions regarding the involvement of brain regions in the occurrence of the orthographic consistency effect. The co-activation hypothesis predicts that areas involved in phonological processing and areas involved in orthographic processing will both be active while the re-shaping hypothesis predicts that the consistency effect is only mediated by areas involved in phonological processing.

So far, no neuroimaging evidence exists in favour of either of these hypotheses as existing studies investigating the orthographic consistency effect differ insofar as they used visual stimuli to investigate abstract phonological processing, but not auditory stimuli only (Booth, *et al.*, 2004; Booth, Cho, Burman, & Bitan, 2007; Petersson, Reis, Askelöf, Castro-Caldas, & Ingvar, 2000; Castro-Caldas, Petersson, Reis, Stone-Elander, & Ingvar, 1998 Orfanidou, Marslen-Wilson, & Davis, 2006). However, the authors of one recent study (Cone, Burman, Bitan, Bolger, and Booth, 2008) using auditory rhyme judgements argue in favour of the co-activation hypothesis, as they found activation of the left fusiform gyrus during their auditory task. Although they conclude that this suggests "that orthographic information in children is automatically activated to spoken words even during phonological tasks" (Cone, Burman, Bitan, Bolger, and Booth, 2008, p. 632), it should be noted that the reported activation cluster could also be explained by activation of the fusiform gyrus due to activated semantic processing taking place in this area (Price, & Devlin, 2003).

Current study

The aim of our study was to test the two hypotheses using transcranial magnetic stimulation (TMS). Introduced in 1985 by Barker, Jalinous, and Freeston (1985), TMS is a non-invasive method for stimulating a targeted cortical region transiently and thus is suitable to test whether a selected cortical region is essential for the performance of a given task (Sack, 2006). That creates the unique possibility to assess the causal relevance of the stimulated area for a given task rather than simply correlating brain activity with behaviour as neuroimaging modalities do.

To achieve the stimulation of nervous tissue, a capacitor is used to create a rapidly-changing current, running through a conducting coil, and thus inducing a strong and relatively focal magnetic field under the coil. When the coil is then placed on the scalp, the magnetic field penetrates the skull without resistance and induces an electric field within the nervous tissue beneath, provoking a physiological response (i.e. depolarization and/or spiking) (Jahanshahi & Rothwell, 2000; Pascual-Leone, Walsh, and Rothwell, 2000). Typically, a spatial resolution of 1 – 2 cm in diameter is assumed. (Walsh & Cowey, 2000).

When TMS is used to transiently interfere with the processing in a given area, often referred to as 'virtual lesion', it does not lead to complete inactivation, but rather introduces transient noise into the neural computation being performed. The behaviourally measurable effect can, depending on the cortical region and the task, either be a slowdown in reaction times or a drop in accuracy scores. By comparing one participant's behavioural data in the stimulated and unstimulated conditions, the effects of TMS can be assessed, while other variables are held as constant as possible. However, the basic physiological mechanisms underlying TMS are not yet fully understood, eventually complicating the interpretation of results (Rothwell, 1997; Di

Lazzaro, *et al.*, 1998; Houlden, Schwartz, Tator, Ashby, and MacKay, 1999). Current research suggests that the effect of stimulation depends crucially on the activation state of the neuronal pool before the stimulation is applied (Silvanto & Muggleton, 2008).

By applying TMS stimulation to cortical areas involved in phonological and orthographic processing, we wanted to test whether one or both areas were essential for the occurrence of the orthographic consistency effect. Therefore, we decided to apply TMS stimulation to the left anterior supramarginal gyrus (SMG), a region reliably-known for being involved in phonological processing (Paulesu, Frith, and Frackowiak, 1993; Celsis *et al.*, 1999; Jacquemot, Pallier, LeBihan, Dehaene, & Dupoux, 2003), and to the left posterior fusiform gyrus (FUS), well-established for its role in orthographic processing (McCandliss, Cohen, & Dehaene, 2003; Price & Devlin 2003; Kronbichler, *et al.*, 2004; Dehaene, Cohen, Sigman, & Vinckier, 2005). Additionally, a control site for each of the two critical sites was chosen to ensure that any observed effects were region-specific. The control sites were chosen to be as similar as possible to the experimental sites with regard to non-specific effects of TMS, such as acoustic and somatosensory artefacts. The control site for the SMG was the left intraparietal sulcus (IPS), as it is very close to the SMG and thus leading to similar somatic and auditory sensations during TMS stimulation, while not being involved in phonological processing. The left occipital complex (LOC) was selected as a control site for FUS stimulation, as previous TMS studies have shown that stimulation of LOC does not significantly affect visual word recognition (Duncan, Pattamadilok, Knierim, and Devlin, in preparation), but participants cannot tell LOC from FUS stimulation. Projections of all four stimulation sites are displayed in Figure 1.

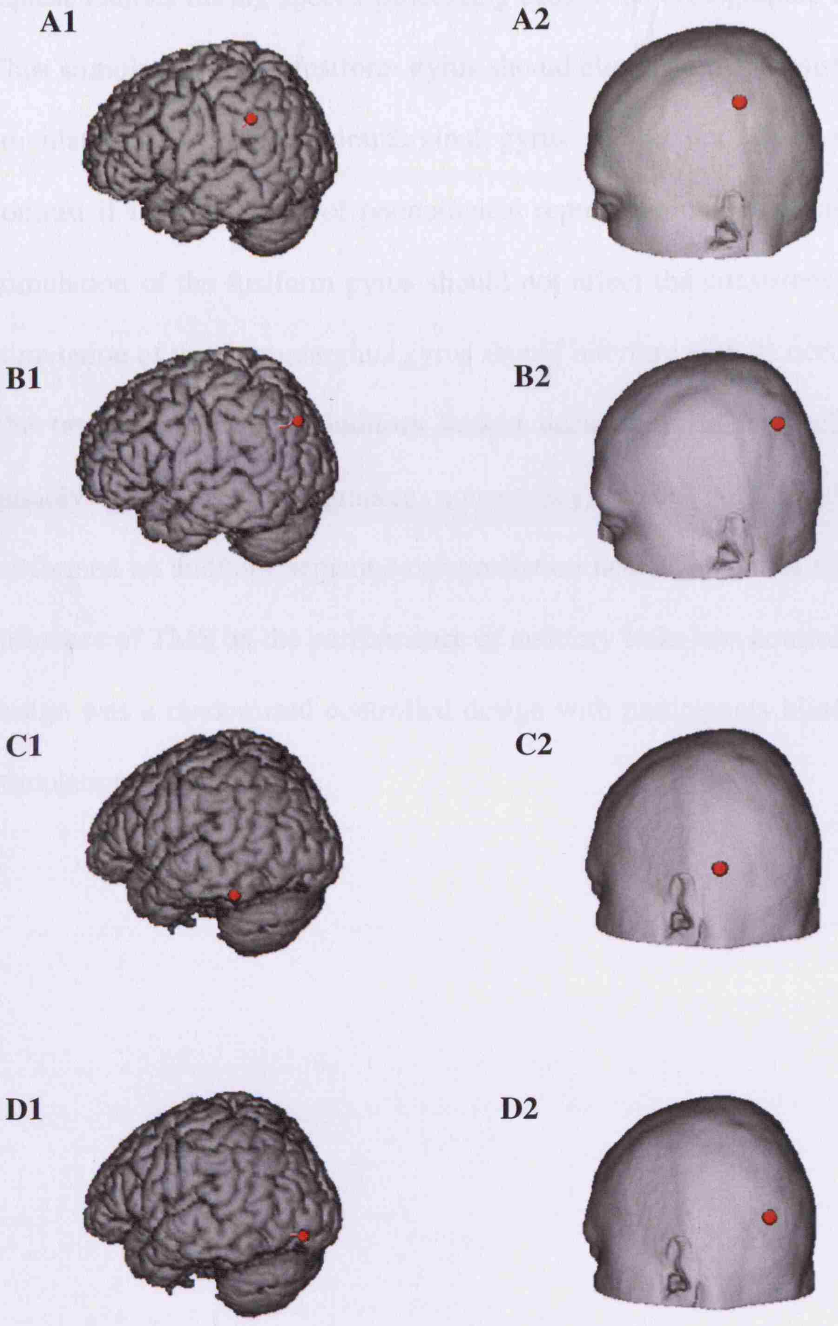

Figure . Projections of the stimulation sites to brain and scalp. A1 Projection for stimulation of the left anterior SMG. A2 Projection for SMG to the scalp. B1 Projection for stimulation of the left IPS to the brain. B2 IPS projection to the scalp. C1 Projection of the left posterior FUS to the brain. C2 Projection of the FUS to the scalp. D1 Projection of the left LOC to the brain. D2 LOC projection to the scalp. All images were generated with the Munster T2T-Converter (http://wwwneuro03.uni-muenster.de/ger/t2tconv/conv3d.html).

The co-activation hypothesis predicts that online-influence of orthographic representations during speech processing causes the orthographic consistency effect. Thus stimulation of the fusiform gyrus should eliminate the consistency effect, while stimulation of the left supramarginal gyrus should not affect its occurrence. In contrast if the re-shaping of phonological representations alone mediates the effect, stimulation of the fusiform gyrus should not affect the consistency effect, however, stimulation of the supramarginal gyrus should interfere with its occurrence.

The task of choice was auditory lexical decision as this speech recognition task reliably elicits an orthographic consistency effect. Additionally, subjects also performed an auditory semantic categorisation task as a control task, so that general influence of TMS on the performance of auditory tasks was controlled. Thus the used design was a randomised controlled design with participants blinded for the chosen stimulation site.

2. Experiments

2.1. Experiment 1

Before conducting the TMS experiment, we conducted a behavioural pilot study in which participants listened to words and pseudowords and had to decide whether the stimulus of each trial was an existing word of English.

2.1.1. Methods

Design

Two different conditions depending on the consistency of a word's rime existed. Rimes were either consistent or inconsistent. All participants were exposed to both conditions. Reaction times and accuracy were recorded.

Participants

Eighteen (12 F, 6 M) healthy English native speakers (18 - 33 years; mean 23 years) participated in the experiment. All participants had no history of language or neurological disorders. Participants gave informed consent after the experimental procedure was explained. The testing sessions lasted about 30 minutes and participants were paid £5. The experiment was approved by the Berkshire Research Ethics Committee (06/Q1602/20).

Material

The stimulus material consisted of 80 monosyllabic words and 80 pseudowords illustrated in Table 2.

Pseudowords were defined as pronounceable utterances without meaning. Words were divided into consistent (N=40) and inconsistent (N=40) conditions. The stimulus material was identical with the material used by Ziegler et *al.* (2008). The two groups of words were matched for word frequency according to the CELEX database (Baayen, Piepenbrock, & van Rijn, 1993), number of letters, number of phonemes, duration, orthographic neighbourhood, number of higher frequency neighbours (Grainger, 1990), body neighbours (Ziegler & Perry, 1998) and phonological neighbourhood (Goldinger, Luce, & Pisoni, 1989). No significant differences in any of these comparisons were found. Additionally, the stimuli were controlled for semantic variables as imageability, meaningfulness and connectivity. For further information about the assessment of these parameters, see Ziegler *et al.* (2008). Pseudowords were selected by using the ARC nonword database (Rastle, Harrington, & Coltheart, 2002). Pseudowords were closely-matched to the words regarding the number of letters (4.5), number of phonemes (3.7), orthographic neighbourhood 5.2) and phonological neighbourhood (8.1). Furthermore, all pseudowords were monosyllabic, orthographically legal and pronounceable according to the ARC nonwords database. The pseudowords were not manipulated regarding consistency. The stimuli (N=160) were divided into four lists each containing 40 stimuli. Each list contained 10 consistent words, 10 inconsistent words and 20 pseudowords in a randomised order. Additionally, two practice lists with 28 trials in total were used in the beginning to familiarise subjects with the task.

Table . Examples of stimulus material for auditory lexical decision task (A complete list of stimuli can be found in Appendix 1).

Category	Rime	Example
Pseudoword	-	wobe
		pewn
Word	consistent	grade
		soap
Word	inconsistent	bull
		swear

Procedure

Participants listened to auditory stimuli via headphones (Bose,Quiet Comfort2). They were asked to decide whether the stimulus was a real word of English (positive trial) or if it was a pseudoword (negative trial). Responses were given via pressing a button on a button box with the index fingers of each hand. Each trial started with the appearance of a black fixation cross in the middle of the screen for 2000 ms. After the fixation cross disappeared, the auditory stimulus was presented. Participants had 2500 ms to respond. The next trial started immediately after the response was given.

2.1.2. Results

Reaction times (RTs) were measured from stimulus onset till the response was given via button pressing. Accuracy was measured with correct or incorrect responses. If subjects responded more than once, the first recorded response was used. The accuracy scores in both conditions were high (consistent: 88%, SEM 2.4; inconsistent: 90%, SEM 2.1) and did not differ significantly ($t(17) = -1.699$, $p = 0.11$, two-tailed).

Only the correct trials were included in the RT analyses. Mean reaction times per subject per condition were calculated and outliers – responses faster or slower than 3 standard deviations from the mean – were excluded (<1%). Additionally, 3 items with poor accuracy (<60%) over all subjects were removed ('puss', 'dose', 'squaw'). Figure 2 shows the mean reaction times for items with consistent and inconsistent rimes. As expected, participants responded faster for consistent than for inconsistent rimes (difference 43 ms), thus leading to the occurrence of the orthographic consistency effect. The effect was significant ($t(17) = -3.142$, $p < 0.05$, two-tailed).

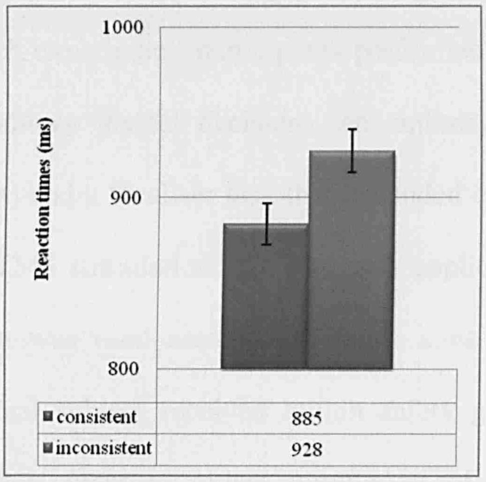

Figure . Results of Experiment 1. Inconsistent rimes lead to 43 ms longer reaction times than consistent rimes. Standard errors of the mean was corrected for repeated measures (Loftus, &Masson, 1994).

2.1.3. Discussion

The RT results replicated previous findings and demonstrated an orthographic consistency effect thus illustrating that stimuli and task were appropriate to elicitate the effect. However, the accuracy data did not show significant differences between the consistent and the inconsistent items suggesting that the effect does influence the time needed to respond, but not the task's level of difficulty. Although the consistency effect was significant across the group, inspection of individual subject's data revealed that 17% of the subjects (3/18) did not show slower reaction times for words with inconsistent rime compared to words with consistent rime in their individual RTs. This information had to be taken into account when designing the TMS experiments to avoid misinterpretation of data by evaluating the effects of TMS in subjects who did not show a consistency effect without TMS. Thus, the lack of the consistency effect in the noTMS condition was defined as an exclusion criterion for the TMS experiments.

2.2. TMS study

Two TMS experiments were performed which primarily differed in the stimulated sites. In each experiment, participants performed three different tasks: an experimental task (auditory lexical decision), an auditory control task (auditory semantic categorisation) and a localiser task that depended on the chosen stimulation site. During the tasks TMS stimulation was randomly applied in half of the trials. A between-subject design was used across stimulation sites to keep the amount of stimulation an individual subject received within safety guidelines (Wassermann, 1998). Thus, participants received either stimulation of the critical site (SMG stimulation in Experiment 2; FUS stimulation in Experiment 3) or of the control site (IPS stimulation in Experiment 2; LOC stimulation in Experiment 3).

Apparatus

A Magstim Rapid^2 stimulator (Magstim, Whitland, UK) with a 70mm figure-of-eight coil was used to deliver the stimulation. The program that controlled stimulus presentations also triggered the TMS pulses. Positioning of the coil was supported by a frameless stereotaxic localising system (BrainSight Software, Rogue Research, Montreal, Canada) in combination with a Polaris Vicra infrared camera (Northern Digital, Waterloo, Ontario, Canada).

2.3. Experiment 2

2.3.1. Methods

Design

There were eight conditions, corresponding to the permutations of the three independent variables: Site (stimulation applied to the SMG or the IPS), Stimulation (trials with or without TMS), and orthographic consistency of the rime (consistent or inconsistent spelling). Each participant participated in four conditions (TMS and noTMS, consistent and inconsistent rimes) because Site was a between-subject condition. The two stimulation sites for this experiment are shown in Figure 3.

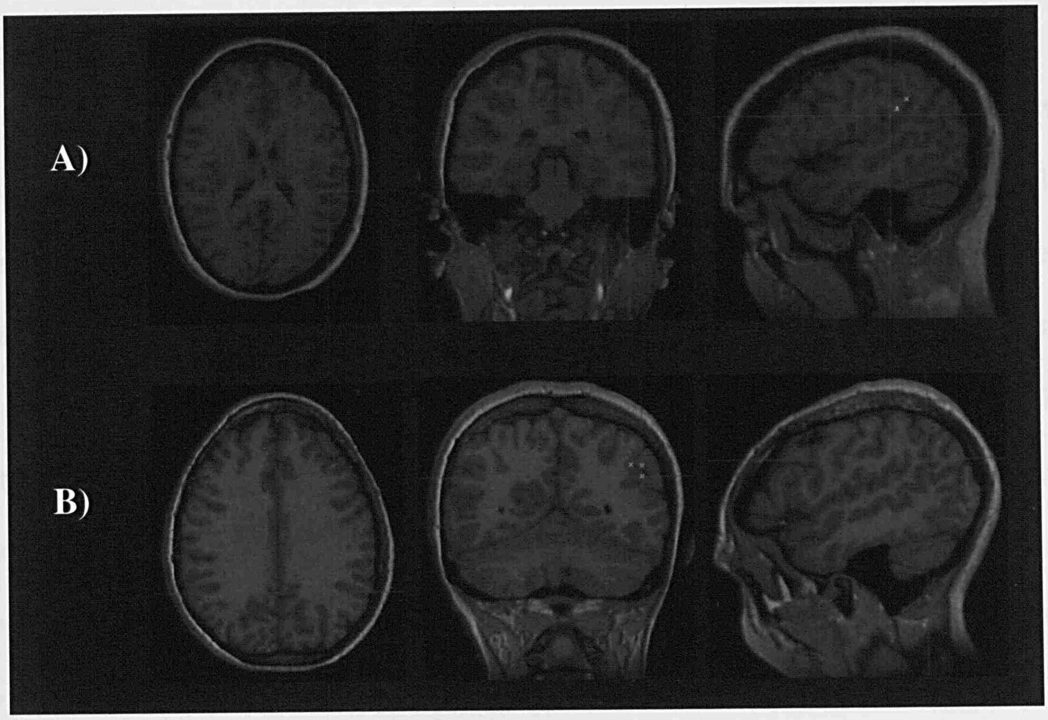

Figure . TMS sites in Experiment 2. A) The frameless stereotaxy for left SMG stimulation in one subject. B) The frameless stereotaxy for left IPS stimulation in one subject. Planes of section from left to right: horizontal, coronal, sagittal. The green crosshairs indicate the location of the maximum field intensity as it intersects the underlying cortex.

Participants

Twenty-one (10 F, 11 M) healthy, right-handed English native speakers (19 - 38 years; mean age 26) participated. All participants had no personal or familial history of a neurological or language-related disorder and all fulfilled the TMS screening criteria, including no family history of epilepsy. All participants gave informed consent after the experimental procedure was explained. The testing sessions lasted between 60 and 90 minutes and all participants were paid for their participation. The experiment was approved by the Berkshire Research Ethics Committee (06/Q1602/20).

None of the participants of the TMS study also participated in the behavioural experiment.

TMS application

Stimulation was applied at a subject's active motor threshold. The active motor threshold was defined as the stimulation intensity needed to activate the muscles of the subject's right hand by applying single pulses over the left motor cortex. Each subject's motor threshold was assessed at the beginning of the testing session. As soon as TMS-induced movement of the hand muscles was observed, the intensity was lowered gradually. The lowest intensity to elicit visual muscle movements on 50% of the trials was used for the main tasks. In all tasks, TMS was applied in 50% of the trials in a semi-randomised fashion, such that there were not more than three trials with or without TMS in a row. Stimulation consisted of trains of four pulses that were applied at a frequency of 10 Hz, so that there were pulses at

0, 100, 200, and 300 ms after stimulus onset. The stimulation parameters were always well within the established TMS safety guidelines (Wassermann, 1998).

TMS localisation

T1-weighted MRI scans were available for all subjects allowing us to co-register each subject with their structural scan and to mark the scalp locations overlying the desired stimulation site using Brainsight. Three markers were set based on anatomy and a localiser task was used to assure the region's functional involvement. Markers were set to cover all regions of a chosen area. Examples for the setting of setting of markers are displayed in Figure 4. For example, for the marking within the anterior supramarginal gyrus, the first marker was set on the part that was per definition more anterior, a second marker was set in the middle of the anterior supramarginal gyrus, and a third marker was set on a more posterior part of the anterior supramarginal gyrus (see Figure 4 and Figure 3A). For functional localisation, one of these markers was stimulated while participants performed a visual rhyme judgement task - deciding whether a pair of written words rhymed or not. Stimuli were manipulated with regard to correspondence between sound and spelling, so that it was not possible to rely on orthography only. There were four conditions: rhyming pairs with the same spelling ('house'- 'mouse'), rhyming pairs with different spellings ('fight'-'kite'), non-rhyming pairs with identical spelling ('deaf' - 'leaf') and non-rhyming pairs with different spelling ('bug'- 'high'). Thus, participants could not rely on orthography only, but had to access the words' phonological representation to perform the task. Eight lists where balanced for the different conditions and thus consequently for congruent and incongruent trials. One practice list was used to familiarise subjects with the task, while another allowed the subjects to become accustomed to the sensation of stimulation. After the presentation of a red fixation cross for 1000 ms, a pair of written words appeared simultaneously on the screen for 500 ms, so that one word was placed above and the other word below a white cross. Immediately after the words disappeared, the screen turned black and participants had 2000 ms to decide whether the words rhymed or not, before the next trial started. Participants indicated their response with a button press. When stimulation of SMG led to a consistent slowdown measured by median and mean reaction times over three lists, then the site was marked and used as the stimulation site for either the experimental or the control task, whose order was counter-balanced across subjects. As IPS was intended as a control site, stimulation was not expected to increase RTs. Consequently, a marker within the IPS was selected when a decrease in reaction times occurred in two out of three lists.

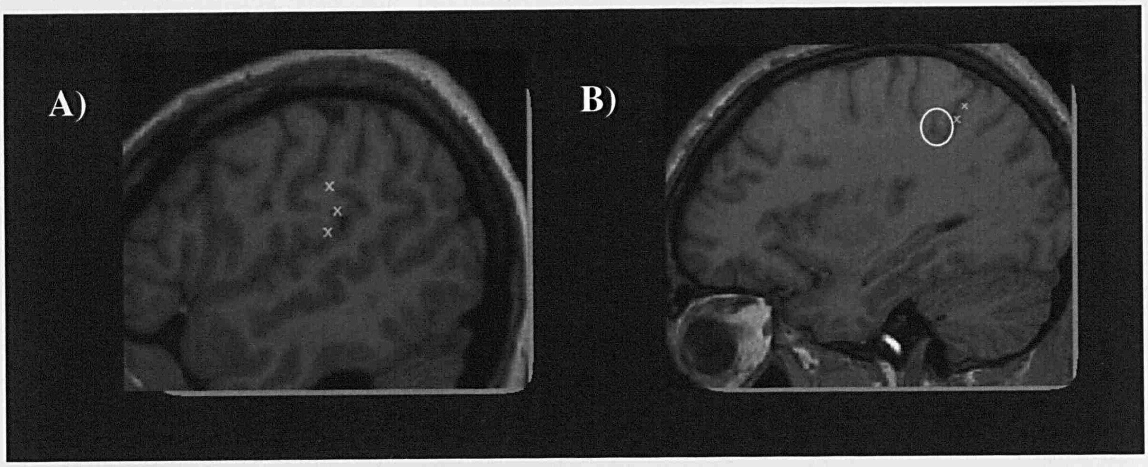

Figure . Marking based on anatomy. A) Three different markers were placed within the SMG of one participant. B) Three markers were assigned within the IPS of one participant. The yellow circle indicated that the red marker was the one selected for stimulation during the task.

Experimental task

Subjects performed a standard auditory lexical decision task, identical with the one in the behavioural study.

Material

The same material as in the behavioural experiment was used. Stimuli were presented through an earphone within the right ear (Sennheiser CX 300-B). An earplug was provided for the left ear to help to minimise the TMS noise and to focus on the stimuli presented in the right ear. Stimuli were divided into four lists with two buffer trials in the beginning of each list. Two practice lists were provided. One list was without TMS, while the second's purpose was to practice performing the task while receiving TMS stimulation.

Procedure

Each trial started with a red fixation cross appearing in the middle of a black screen for 1000 ms. Then the cross disappeared and an auditory stimulus was presented. Participants had 2500 ms from stimulus onset to respond before the next trial started, leading to total trial duration of 3.5 sec. The procedure is illustrated in Figure 5. Thus, the duration of each list was about 2.5 minutes. Responses were given on the numerical keypad of the presentation computer and all subjects responded with their right hand, using their index and their middle finger.

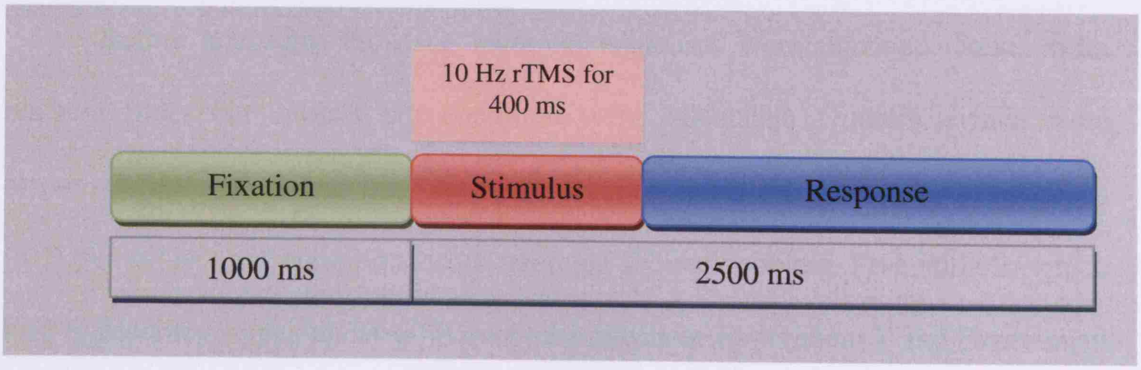

Figure . Trial procedure for the experimental and the control task. After a fixation cross appeared on the screen for 1000 ms, the auditory stimulus was presented. In TMS trials, rTMS was applied for 400 ms starting with stimulus onset. From stimulus onset on, participants had 2500 ms to respond.

Control Task

A semantic categorisation was used as a control task. Here, participants decided whether an auditorily presented word referred to something that was touchable or not, in order to focus their attention on the underlying meaning of the word: abstract versus concrete. The stimuli consisted of 80 monosyllabic English words, divided into 40 positive (touchable) and 40 negative (non-touchable) trials. The stimuli were presented in two lists each containing 40 trials. Lists were balanced for positive and negative trials. Additionally, each list included two buffer trials in the beginning. A practice list was used to familiarise subjects with the task. No TMS stimulation was applied during the practice. The presentation of stimuli and the settings for responses were held constant with the lexical decision task, such that after a fixation cross was presented on the screen for 1000 ms, the screen turned blank and the auditory stimulus was presented. From stimulus onset on, participants had 2500 ms to give their response. In the TMS trials, 400 ms of rTMS were applied beginning with stimulus onset.

2.3.2. Results

Experimental task

Before analysing the data, incorrect responses were removed. Next, mean reaction times per subject per condition were calculated. Outliers, which were responses faster or slower than the mean reaction times plus 3 standard deviations (SD) per subject per condition, were removed for each subject. Five stimuli, which lead to accuracy scores under 60% over all subjects of Experiment 1 and Experiment 2, were excluded ('frost', 'malt', 'puss', 'salve', 'squaw'). Thereafter, RTs and accuracy scores were analysed. To begin, subjects who did not show an orthographic consistency effect in the absence of TMS (n=3) were excluded. This was necessary in order to ensure that any putative TMS effects on consistency all occurred in the context of an actual orthographic consistency effect. Thus, 18 subjects remained for the final analysis. Ten of them were stimulated at the SMG (experimental group) and 8 were stimulated at the IPS (control group). Table 3 displays the mean accuracy scores in percent per condition.

Table . Mean accuracy scores for experimental task in Experiment 2 in percent.

	SMG		IPS	
	noTMS	TMS	noTMS	TMS
Consistent	90%	88%	94%	93%
inconsistent	89%	84%	92%	93%

High accuracy scores were obtained across all conditions illustrating, that the application of TMS did not hinder the performance. Accuracy scores were subsequently analysed with a factorial mixed-design 2 x 2 x 2 analysis of variance (ANOVA) examining the effects of the within-subject factors Stimulation (noTMS vs. TMS) and, Consistency (consistent vs. inconsistent), and the between-subjects factor Site (IPS vs. SMG). No significant differences due to the manipulated factors Site, Stimulation and Consistency were found regarding the accuracy of responses (TMS: $F(1,16) = 1.386$, $p = .256$; Site: $F(1, 16) = 1.604$, $p = .223$; all interaction terms Fs < 1). Thus, accuracy scores were not affected by the consistency of the word's rime or by stimulation. This was the case for individuals at both stimulation sites, so that there was also no effect of site.

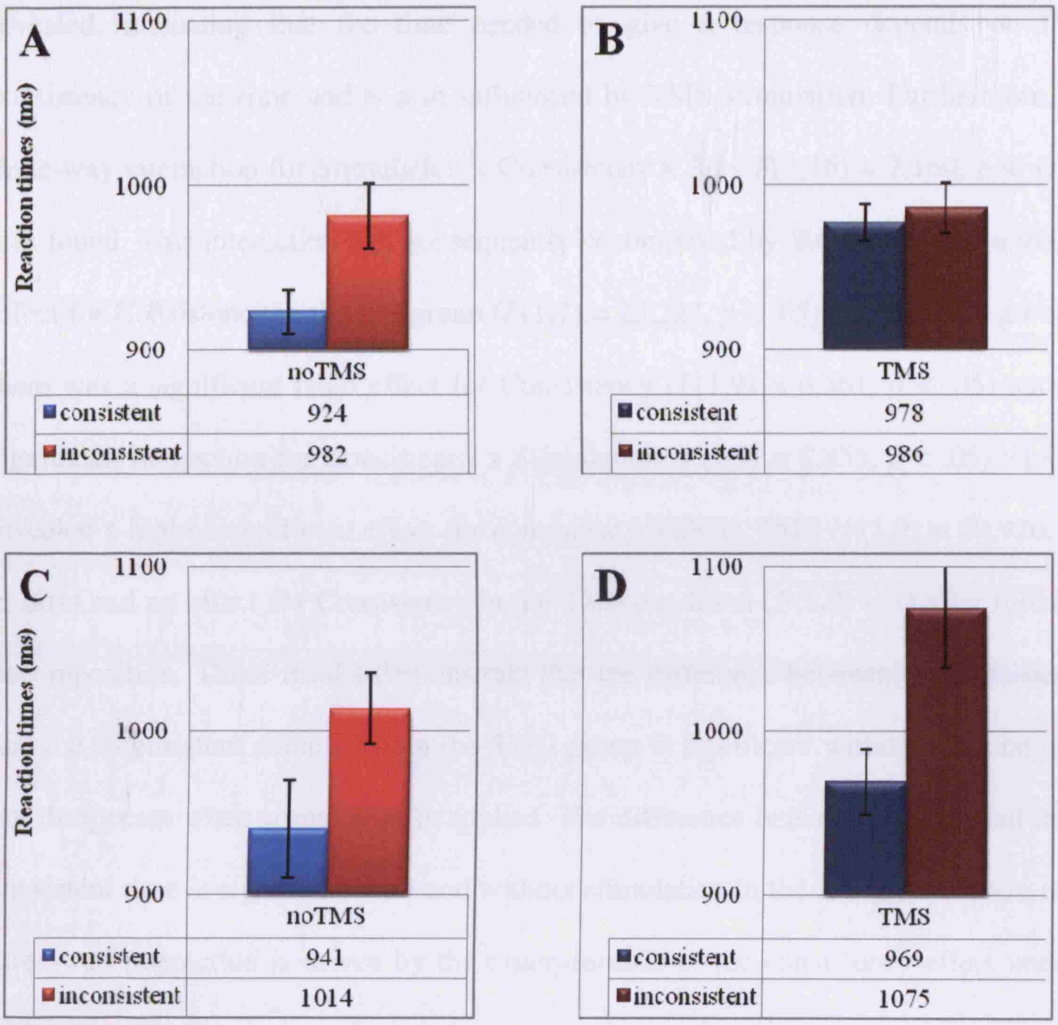

Figure . Results of the experimental task in Experiment 2. **A** Mean reaction times for trials without stimulation in the group receiving SMG stimulation. Inconsistent rimes lead to longer reaction times than consistent rimes. **B** Mean reaction times for trials with SMG stimulation. The difference between consistent and inconsistent rimes disappears. **C** Mean reaction times for trials without stimulation in the group receiving IPS stimulation. Inconsistent rimes lead to longer reaction times than consistent rimes. **D** Mean reaction times for trials with IPS stimulation. Inconsistent rimes show longer reaction times than consistent rimes. Standard errors of the mean were corrected for repeated measures (Loftus, & Masson, 1994).

Figure 6A shows a 58 ms consistency effect in the SMG noTMS condition and a 73 ms consistency effect in the IPS noTMS condition (Figure 6C) This consistency disappears with SMG stimulation (8 ms) (Figure 6B), but is not affected by IPS stimulation (106 ms) (Figure 6D). When analysed in an identical fashion as accuracy scores, a highly significant main effect of Consistency, $F(1,16) = 31.056$, $p < .001$ and a significant main effect for Stimulation, $F(1,16) = 4.536$, $p < .05$ were revealed, indicating that the time needed to give a response depends on the consistency of the rime and is also influenced by TMS stimulation. Furthermore, a three-way interaction for Stimulation x Consistency x Site, $F(1,16) = 7.160$, $p < .05$) was found. This interaction was subsequently decomposed by Site, leading to a main effect for Consistency in the IPS group ($F(1,7) = 23.224$, $p < .05$). In the SMG group, there was a significant main effect for Consistency ($F(1,9) = 6.561$, $p < .05$) and a significant interaction for Consistency x Stimulation ($F(1,9) = 8.855$, $p < .05$) which revealed a highly significant effect for consistency without TMS ($F(1,9) = 29.920$, $p < .001$) and no effect for Consistency in the TMS condition ($F(1,9) < 1$) after further decomposition. These results demonstrate that the difference between the consistent and the inconsistent stimuli within the SMG group is significant without stimulation, but disappears when stimulation is applied. The difference between inconsistent and consistent rime is significant with and without stimulation in the IPS group. Thus, the three-way interaction is driven by the disappearance of the consistency effect under SMG stimulation.

Semantic control task

The data from the semantic control task was analysed using a mixed 2 x 2 ANOVA with the between factor Site (SMG vs. IPS) and the within factor Stimulation (noTMS vs. TMS). Previous to statistical analyses, incorrect trials and outliers (> mean +/- 3 SD) were removed. The mean accuracy scores of the control task are displayed in Table 4. They do not differ significantly due to the manipulated variables (Stimulation: $F(1,16) = 1.099$, $p = .310$; Site: $F(1,16) < 1$; Stimulation x Site: $F(1,16) = 1.361$, $p = .260$). Although the task was a decision about abstract and concrete words, we decided not to analyse the data taking the abstractness of a word into account. As it is known that there are differences due to the level of abstractness (Barsalou, 1999; Paivio, 1991; Schwanenflugel, 1991) which were not specifically relevant to either hypothesis, we did not want to get confounded by these. Therefore, we decided that it was most appropriate to combine the word categories for analysis.

Table . Mean accuracy for control task in Experiment 2 in percent.

SMG		IPS	
noTMS	TMS	noTMS	TMS
88%	88%	89%	85%

The mean RTs shown in Figure 7 did not reveal any significant differences when analysed with a 2x2 analysis (Stimulation: noTMS vs. TMS; Site: SMG vs. IPS) (Stimulation: $F(1,16) = 2.922$, $p = .107$; Site: $F(1,16) = 1.387$, $p = .256$; Stimulation x Site: $F(1,16) < 1$), indicating that stimulation does not have an effect on subjects' accuracy. Furthermore, no difference between the SMG and the IPS group is revealed.

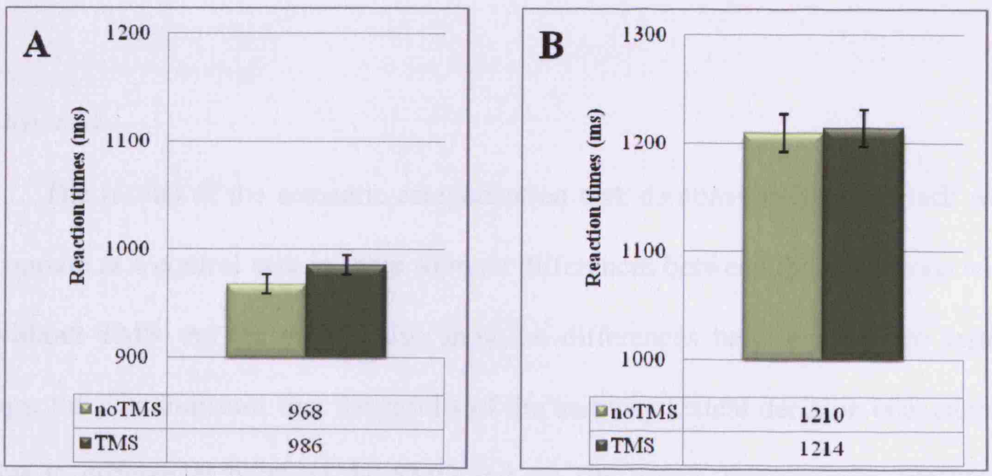

Figure . Results of the control task in Experiment 2. A Results for stimulation of the SMG. B Results for stimulation of the IPS. rTMS does not affect the reaction times in both groups. Standard errors of the mean were corrected for repeated measures (Loftus, & Masson, 1994).

2.3.3. Discussion

A comparison of the RTs and accuracy scores across the SMG and the IPS group shows that the IPS group is slower across all conditions than the SMG group, but also shows higher accuracy scores, indicating a trade-off between accuracy and pace. However, the accuracy scores in both groups were not affected by the consistency manipulation. This finding is consistent with the results of the behavioural study, although early experiments also reported a drop in accuracy scores for inconsistent rimes (Ziegler & Ferrand, 1998).

The major finding, however, is the site-dependent manipulation of the orthographic consistency effect by TMS stimulation. The significant three-way interaction reveals that the consistency effect only disappears if TMS is applied to the SMG. In contrast, TMS stimulation of the IPS does not affect the occurrence of the orthographic consistency effect. Further inspection of the reaction times shows a disappearance of the effect because a slowdown for consistent rimes occurs under TMS stimulation. The mean reaction times of inconsistent words stay constant, suggesting that the TMS stimulation preferentially affects the processing of consistent words.

Control task

The results of the semantic categorisation task demonstrate that the task was appropriate as a control task as there were no differences between the conditions with or without TMS. As the results also show no differences between the two tested groups, the data indicates that the results of the auditory lexical decision task cannot be due to differences between the SMG and the IPS group. Interestingly, the mean reaction times of both groups were slower when performing the control task, suggesting that more time is needed to perform a task requiring semantic access. In conclusion, the control task illustrates that TMS did not interfere with word processing in general.

2.4. Experiment 3

2.4.1. Methods

Design

The design was identical with Experiment 2 apart from the chosen stimulation sites (left posterior fusiform gyrus (FUS) or lateral occipital complex (LOC)) and the localisation procedures.

Participants

Twenty-six (13 F, 13 M) healthy, right-handed English native speakers (18 - 45 years; mean age 25) participated. As in Experiment 2, all participants had no personal or familial history of a neurological or language-related disorder and all fulfilled the TMS screening criteria, including no family history of epilepsy. All participants gave informed consent after the experimental procedure was explained. The testing sessions lasted about 60 minutes and all participants were paid for their participation. The experiment was approved by the Berkshire Research Ethics Committee (06/Q1602/20).

TMS application

The TMS application was held constant with Experiment 2.

TMS localisation

A functional localiser was used to select the appropriate TMS target. As TMS stimulation of the fusiform gyrus can provoke discomfort in some subjects, we decided to use functional Magnetic Resonance Imaging (fMRI) to localise the TMS targets as this reduces the applied number of TMS pulses compared to functional localisation using TMS session as was done in the previous experiment. For that purpose, subjects performed an fMRI experiment in a different session. Because the fMRI data are not specifically important to the current results, they are only explained briefly here.

A oneback task was used within the scanner where subjects were instructed to press a button whenever they detected a repeat. The stimuli consisted of four different categories of visual stimuli: written words, pictures of common objects, scrambled pictures of the same objects, and consonant letter strings. Stimuli were presented in a block design and each block consisted of 16 trials from a single category. There where two runs of the experiment and each run entailed six blocks per category leading to a total of 192 stimuli per category. The order of the runs was counterbalanced across subjects. A trial began with a 650 ms fixation cross followed by the stimulus for 350 ms. One stimulus was presented every second. Between different blocks were resting periods in which a fixation cross was displayed for 16 s. Word stimuli consisted of mono- or bi-syllabic 4 or 5 letter words. Object stimuli consisted of black and white pictures (200 × 250 pixels) of easily recognisable objects. The pictures of scrambled objects were generated by dividing the object stimuli into 10 × 10 pixel squares and permuting their placement within the image. None of the resulting images were recognisable after scrambling. Consonant letter strings were unpronounceable strings randomly generated to exactly match the length of the word stimuli.

Whole-brain imaging was performed on a Siemens 1.5 Tesla MR scanner at the Birkbeck-UCL NeuroImaging Centre in London. The functional data were acquired in two runs, each lasting 8 min with a gradient-echo EPI sequence (TR = 3000ms; TE = 50ms, FOV=192 x 192, matrix = 64 x 64) giving a notion resolution of 3 x 3 x 3mm. In addition, a high-resolution anatomical scan was acquired (T1-weighted FLASH, TR = 12 ms; TE = 5.6m; 1mm^3 resolution) for anatomically localizing activations and to accurately target TMS stimulation sites in each individual using a frameless stereotaxic system (BrainSight).

The functional imaging data were analysed using FSL (www.fmrib.ox.ac.uk/fsl). After deleting the first two volumes of each run to allow for T1 equilibrium, the functional images were realigned to correct for small head movements (Jenkinson, Bannister, Brady, & Smith, 2002). The images were then smoothed with a 5mm FWHM Gaussian filter and pre-whitened to remove temporal auto-correlation (Woolrich, Ripley, Brady, & Smith, 2001). The resulting images were entered into a subject-specific general linear model with four conditions of interest corresponding to the four categories of visual stimuli. Blocks were convolved with a double gamma “canonical HRF” (Glover, 1999) to generate the main regressors. In addition, the estimated motion parameters were entered in as covariates of no interest, to reduce structured noise due to minor head motion. Linear contrasts were used to identify the three TMS target sites within each subject: FUS by contrasting words to rest and LOC by contrasting objects to scrambled objects. Finally, the functional images were registered to each participant’s individual structural scan using a 12 DoF affine transformation (Jenkinson, Bannister, Brady, &

Smith, 2002) in order to identify two TMS target sites (FUS and LOC) in the left cerebral hemisphere. Examples for chosen stimulation sites based on functional activation patterns are shown in Figure 8.

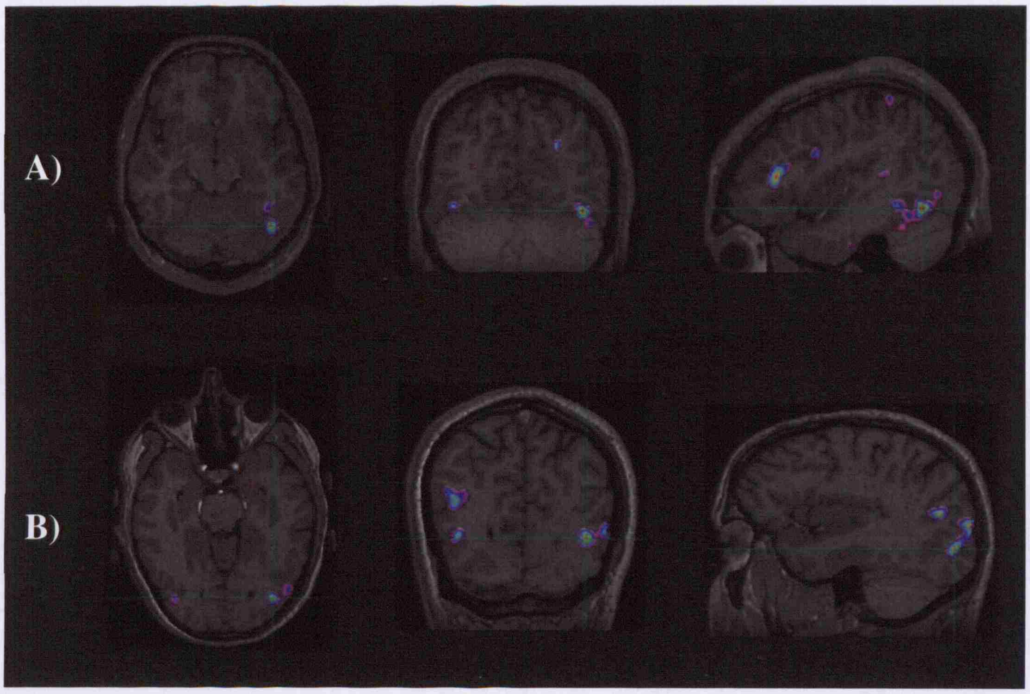

Figure . TMS sites in Experiment 3. A) The frameless stereotaxy for left FUS stimulation in one subject. B) The frameless stereotaxy for left LOC stimulation in one subject. Planes of section from left to right: horizontal, coronal, sagittal. The green crosshairs indicate the location of the maximum field intensity as it intersects the underlying cortex.

Experimental and control tasks

The task, the stimuli and the procedures were identical to those outlined in Experiment 2.

An additional task was used to ensure that the stimulation of the fusiform site identified by fMRI had a behaviourally measurable effect on orthographic processing. Here we used visual lexical decision as we have previously shown that stimulation of the left posterior fusiform preferentially disrupts word, but not pseudoword, reading (Duncan, Pattamadilok, Knierim, and Devlin, in preparation). This was performed after the auditory tasks to avoid alerting participants to the potential relevance of orthographic representations. During the task, written words and pseudowords were presented on the screen and participants were asked to decide whether the stimulus was an existing English word. Reaction times were measured. For FUS but not LOC stimulation, a TMS-induced slowdown in the word condition was expected.

2.4.2. Results

The same inclusion/exclusion criterion was applied here that were used for Experiment 1, namely the requirement that each participant shows an orthographic consistency effect in the trials without stimulation. Due to this criterion 6 subjects had to be excluded. Furthermore, 3 subjects were not included in the analysis as we were not able to assess their active motor threshold. Finally, 2 subjects failed to show a slow down in the visual lexical decision task, so that we could not demonstrate that the chosen stimulation site influences orthographic processing. After applying these exclusion criteria, 15 subjects (8 F, 7 M; age 19-38 years, mean 28) remained for final analysis. From these 15 subjects, 8 received stimulation of the FUS (experimental group) and 7 received stimulation of the LOC (control group).

As before, only correct trials were included in the RT analysis and RTs shorter or longer than the mean RT +/- 3SD were discarded. This was done, by subject, separately for each stimulus type (as defined by the presence of TMS stimulation and consistency). Five items with poor accuracy (<60 %) over all TMS participants (all participants Experiment 2 and Experiment 3) were excluded ('frost', 'malt', 'puss', 'salve', 'squaw'). The accuracy scores for the experimental task are shown in Table 5.

Table . Mean accuracy for experimental task in Experiment 3 in percent.

	FUS		LOC	
	noTMS	TMS	noTMS	TMS
Consistent	83%	89%	87%	91%
Inconsistent	88%	90%	88%	86%

A mixed 2 x 2 x 2 ANOVA examined the effects of Stimulation, Consistency, and Site but did not reveal any significant main effects (Consistency: $F(1,13) = 1.759$, $p = .208$; TMS: $F(1,13) < 1$; Site: $F(1, 13) < 1$). The Consistency x Stimulation interaction, however reached significance, $F(1,13) = 4.905$, $p = .045$. Further analyses of this interaction showed that the consistency effect on noTMS trials almost reached significance $F(1,13) = 3.863$, $p = .071$ (noTMS: 2 x 2 ANOVA (Site x Consistency). No other main effects or interactions were significant (all *F*s <1). The data shows that in the FUS group, higher mean accuracy scores are obtained for inconsistent words than for consistent words. In the LOC group, the pattern is reversed. A comparison of the noTMS conditions with the TMS conditions reveals that in the FUS group TMS leads to a consistent increase in accuracy scores. In the LOC group, accuracy scores are increased for consistent words and stimulation, but decreased for inconsistent words and stimulation. To sum up, no consistent pattern seems to underly the interaction.

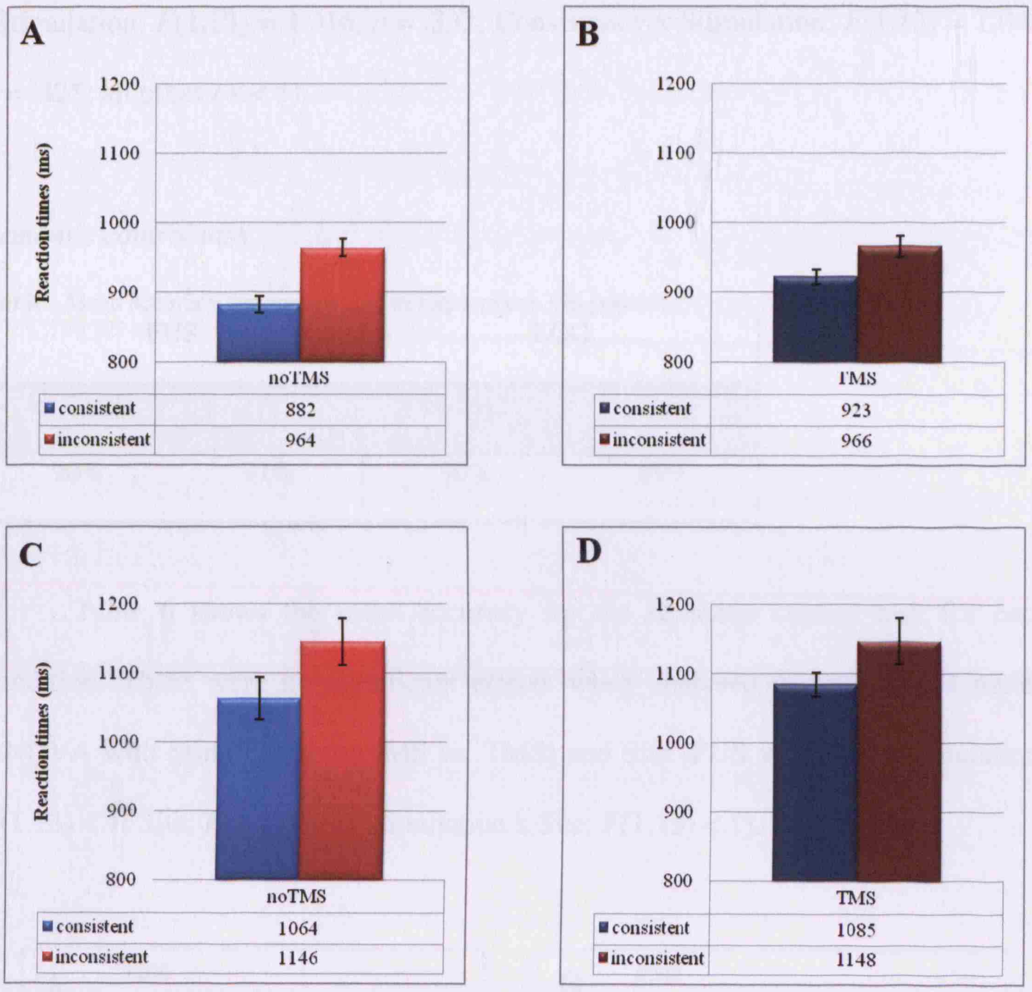

Figure . Results for the experimental task in Experiment 3. **A** Mean reaction times for trials without stimulation in the group receiving FUS stimulation. Inconsistent rimes lead to longer reaction times than consistent rimes. **B** Mean reaction times for trials with FUS stimulation. The difference between consistent and inconsistent rimes remains stable. **C** Mean reaction times for trials without stimulation in the group receiving LOC stimulation. Inconsistent rimes lead to longer reaction times than consistent rimes. **D** Mean reaction times for trials with LOC stimulation. Inconsistent rimes show longer reaction times than consistent rimes. Standard errors of the mean were corrected for repeated measures (Loftus, & Masson, 1994).

The RT data displayed in Figure 9 show that the LOC group was slower across all conditions than the FUS group. Both groups show consistency effects independent from Stimulation. When analysed, the differences between consistent and inconsistent conditions lead to a highly significant main effect of Consistency, $F(1,13) = 34.848$, $p < .001$. Furthermore, there was a significant main effect for Site $F(1,13) = 9.834$, $p < .05$, confirming that RTs from the LOC site were longer than those in the FUS site. No other main effects nor interactions reached significance

(Stimulation: $F(1,13) = 1.016$, $p = .332$; Consistency x Stimulation: $F(1,13) = 1.045$, $p = .325$; all other Fs < 1).

Semantic control task

Table . Mean accuracy for control task in Experiment 3 in percent.

FUS		LOC	
noTMS	TMS	noTMS	TMS
90%	91%	90%	89%

Table 6 shows the mean accuracy for the semantic control task for each condition. There were no significant effects when analysed using a 2 x 2 mixed ANOVA with Stimulation (noTMS vs. TMS) and Site (FUS vs. LOC) (Stimulation: $F(1,13) < 1$; Site: $F(1,13) < 1$; Stimulation x Site: $F(1,13) < 1$).

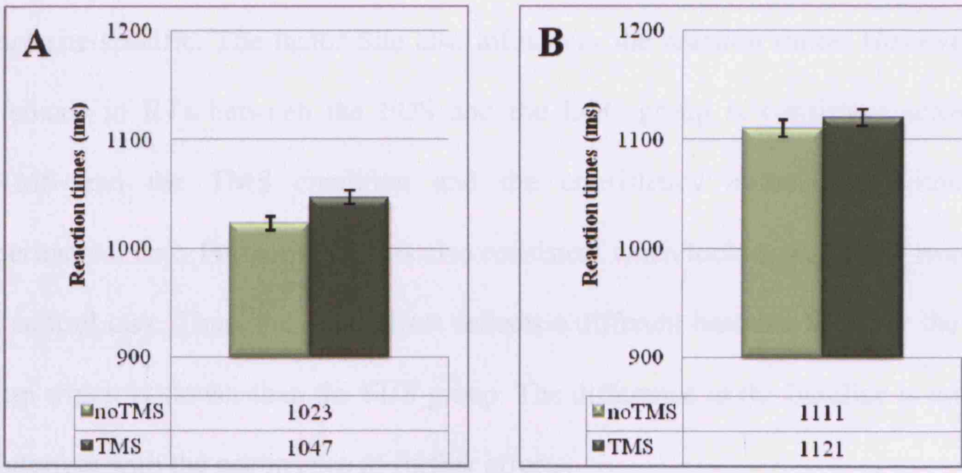

Figure . Results of the control task in Experiment 3. A Results for stimulation of the FUS. B Results for stimulation of the LOC. rTMS stimulation does not affect the reaction times in both groups. Standard errors of the mean were corrected for repeated measures (Loftus, & Masson, 1994).

Mean RTs show that the LOC group was slower than the FUS group independent from stimulation (Figure 10). This difference reached significance when analysed with a 2 x 2 ANOVA (Site: $F(1,13) = 9.876$, $p < .05$). No other significant effects were found (Stimulation: $F(1,13) < 1$; Stimulation x Site: $F(1,13) < 1$), meaning that there was a significant difference between the two groups, but no difference due to TMS. The analysis of the accuracy scores shows high over all accuracy and a significant interaction between Consistency and Stimulation. Inspection of the data suggests that this reflects the higher accuracy scores for consistent rimes with stimulation than without. However, the comparison between consistent rimes with and without stimulation did not reach significance.

2.4.3. Discussion

The RT data show a highly significant main effect for Consistency and a main effect for Site, but no interactions. In other words, the orthographic consistency effect is present in the noTMS and in the TMS conditions in both groups and is thus independent from the application of TMS stimulation. The consistency effect is reduced in its size in the FUS and the LOC group, thus suggesting that the reduction is not site-specific. The factor Site also influences the reaction times. However, the difference in RTs between the FUS and the LOC group is consistent across the noTMS and the TMS condition and the consistency stimulation within the experimental task. Furthermore, it is also consistent when looking at the RT results of the control task. Thus, the main effect reflects a different baseline level for the LOC group which is slower than the FUS group. The difference in the baseline is unlikely to interfere with the occurrence of further effects.

Control task

As in the previous experiment, no differences between the noTMS and the TMS conditions were measurable, demonstrating that TMS to FUS and LOC did not interfere with the performance of the task and even more importantly, with the processing of auditory stimuli in general. Although both groups' mean reaction times were slower in the control task compared to the auditory lexical decision task, the LOC group was significantly slower than the FUS group. Taking the limited sample size into account, the main effect for Site in both the experimental and the control tasks probably reflects that by chance the participants of the LOC group were slower responders than those in the FUS group.

3. General discussion

Our results demonstrate that the occurrence of the orthographic consistency effect can be modulated by applying TMS to the left anterior SMG, a site known for its involvement in phonological processing - indicating that the SMG is causally involved in the effect's occurrence. In contrast, stimulation of the left posterior fusiform gyrus – a region implicated in orthographic processing – did not significantly affect the orthographic consistency effect. The use of a control task enabled us to exclude the possibility that the observed effects resulted from general TMS-induced interference with processing of auditory stimuli.

We hypothesised that the orthographic consistency effect results either from co-activation of competing orthographic representations ('co-activation hypothesis'), or from the competition between multiple abstract phonological representations for inconsistent rimes that developed after learning to read and write ('re-shaping hypothesis'). With regard to these hypotheses, the results clearly support the re-shaping hypothesis as the orthographic consistency effect was only manipulated by stimulation of a phonological area. Furthermore, they reject the co-activation hypotheses as stimulation of the orthographic site (fusiform gyrus) did not affect on the orthographic consistency effect. This strongly suggests that the activation in the left fusiform gyrus reported by Cone and collaborators (2008) is not due to automatically activated orthographic representations, i.e. an epiphenomenon, but might result from semantic processing taking place in this area.

The consistency effect is caused by longer reaction times for inconsistent rimes relative to consistent rimes. Therefore, the TMS induced elimination of the consistency effect may be the result of: 1. A TMS induced slowdown in consistent words. 2. A TMS induced speedup of inconsistent words. Our data strongly supports the first possibility, as we observed a TMS induced slowdown for consistent rimes (+54 ms with TMS) with no concurrent reaction time change in inconsistent rimes (+4 ms with TMS). This suggests that under normal circumstances consistent rimes have a processing advantage over inconsistent rimes but stimulation of SMG abolishes this advantage.

A speculative explanation is that consistent words possess more fine-grained and more easily accessible phonological representations than inconsistent words, in the sense that they activate only one neural coding network that dominates processing. In contrast, inconsistent rimes elicit the activation of several phonological representations that enter mutual competition. According, a word with a consistent rime such as –ust (e.g. *must*), activates the coding network for the rime –ust. There is only one network, as this rime is always spelt UST. Conversely, if a word like *head* enters the computation, three possible representations of the rime become active. The distinct phonological representations result from the three possible spelling patterns EAD as in *head*, ED as in *wed* and AID as in *said* that were learnt when learning to read and write. The competition of multiple representations results in more processing load which is reflected in longer reaction times. Thus it could be speculated that the acoustic signal acts as a filter determining the resulting activation pattern. TMS stimulation of SMG in this model would thus be to make the processing more difficult either by adding noise to the system or by reducing signal strength (Harris, Clifford, & Miniussi, 2008). The observed behavioural pattern suggests that the processing is only marginally interfered with, so that it is not the computation as such that is challenged – but that facilitative components are lost during stimulation. Neurons within a population are influenced by the tuning of their input filters thus leading to more and less strongly responding neurons to a certain stimulus. Silvanto, Muggleton, Cowey, and Walsh (2007) recently reported that TMS reduces the difference in activity by having a greater effect on the normally less active neurons, resulting in equally active neurons. Applied to our data, this model suggests that during the processing of a consistent rime TMS normally activates less active neuronal networks and thus induces competition. As inconsistent rimes do not have a dominantly-activated coding pattern to begin with, they are less affected by TMS.

Based on our findings, it is possible to introduce a notional hypothesis on the role of left SMG during rime processing. Previous research (Raizada, & Poldrack, 2007) demonstrated that left SMG was "the most categorical processing region" (Raizada, & Poldrack, 2007, p. 738) in a categorical perception task. They assessed selective neuronal amplification for pairs of speech sounds on the continuum between the phonemes /ba/ and /da/. While differences within a category were suppressed (i.e. both stimuli are perceived as the phoneme /ba/), differences crossing the phonemic category were selectively amplified (i.e. one stimulus is perceived as representing the phoneme /ba/, while the other is perceived as representing the phoneme /da/). Raizada and Poldrack (2007) concluded that "the way in which the brain selectively amplifies stimulus differences can help to reveal how its representations of the world are structured" (Raizada, & Poldrack, 2007, p. 738). Thus it is possible that the assumed differences between the representations of words with consistent and words with inconsistent rimes are also expressed by differences in the amplification of the different rime categories. While selective amplification might take place when consistent words are processed, this would not be expected to the same extent for inconsistent rimes. The idea is that selective amplification shapes perceptual categories – here consistent versus inconsistent – and thus emphasises differences between different stimuli. The development of the categories itself was triggered by the process of learning to read and write. This hypothesis has the capacity to exemplify a way in which input from the visual language modality causes the forming of new categories within the auditory language modality. These rime-specific categories can be regarded as a superordinate level to the categorical perception of phonemes. As left SMG is the most categorically processing region for phonemes, it might also be predisposed to fulfil this role on a higher level.

In further research, it would be important to identify the reasons, why the orthographic consistency effect was not present in all subjects. In our experiments, the percentage of participants who did not show the consistency effect varied between 14% and 19% (Experiment 1: 17%; Experiment 2: 14%; Experiment 3: 19%). This could be especially interesting as the size of the consistency effect was correlated of children's reading levels in developmental studies (Ventura, Morais, & Kolinsky, 2007). Therefore, research correlating reading ability and reading strategies in adulthood and presence and form of the consistency effect would be of interest. Furthermore, the specific time window during which the effect can be modulated with TMS could be investigated by using a single- or paired-pulse TMS protocol, where TMS delivered at different time windows, for example 0, 100, 200, 300 ms post-stimulus onset.

To conclude, our data can be explained by assuming that TMS of SMG induces noise into the auditory processing of words, which selectively affects the processing of words with consistent rimes. In conclusion, we demonstrated for the first time that the orthographic consistency effect is mediated at a phonological level presumably because learning to read fundamentally reshapes phonological representations.

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5. Appendix

Appendix . Stimuli for auditory lexical decision task in Experiments 1,2, and 3

Consistent words (N=40)	Inconsistent words (N=40)	Pseudowords (N=160)	
aunt	bald	bilm	naste
blink	beard	blit	nerge
bull	blur	boft	nusk
bush	bomb	brike	pewn
casque	caste	broy	pibe
clash	clerk	clea	plack
clip	cough	clup	pouth
coins	cox	creef	praw
crab	crowd	creer	prife
crisp	deaf	crite	rimp
dish	dune	crub	roft
dive	foul	darb	ront
dose	freak	dimp	scoon
dove	frost	douge	shiff
gloves	grade	drace	skay
golf	gross	droon	sleen
gouge	lamb	dult	slone
gown	monk	felp	smuck
junk	mule	filk	spame
loaf	muse	fleep	sping
malt	mute	flun	spum
math	myth	foms	sterm
moth	plea	frace	sult
pint	priest	frawl	swarp
plug	scone	frip	telp
puss	smear	froat	toft
salve	soap	gesh	toist
shave	spur	glame	tooch
shove	squad	glush	trup
silk	squash	goob	trush
smart	squaw	heafs	tuce
snob	swamp	hench	tunch
soot	swan	hoin	tupe
tape	swear	hoob	vaint
thrill	sweat	jount	veem
tusk	tact	lisk	viss
vague	truce	lomp	wilch
wasp	vase	moint	wobe
wolf	warp	mube	yarm
wounds	wool	muke	yeam